SEASONAL VARIATION IN BISON DISTRIBUTION AND GROUP BEHAVIOR ON OKLAHOMA TALLGRASS PRAIRIE

By

KRYSTEN LYNN SCHULER

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University of Notre Dame

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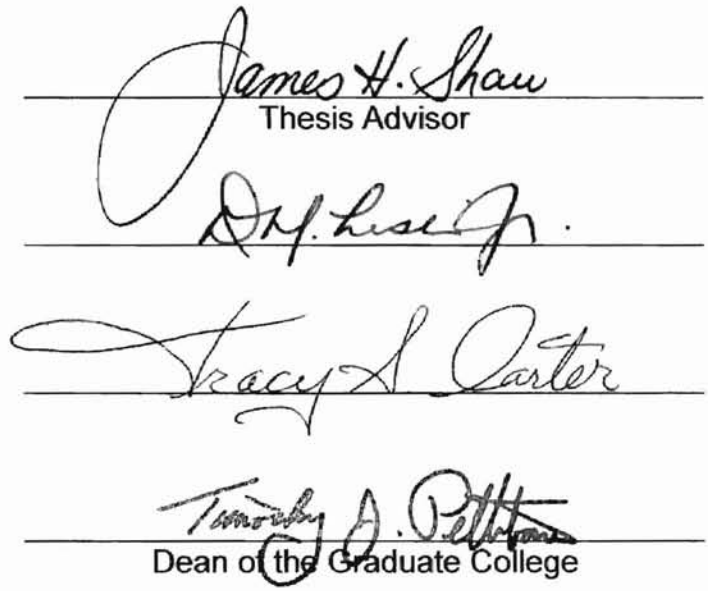

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Dean of the Graduate College

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The question I've been asked most often during my time at Oklahoma State is, "Why did you come to Oklahoma?" The simple answer is that I wanted to study bison. Seeing bison on tallgrass prairie is something that few people have had the opportunity to do since the early pioneers crossed the plains. Little did I know how much time I would spend on those plains, observing the often-illusive bison. I was able to spend copious amounts of time on 1 of the last remaining unplowed tracts of tallgrass prairie. I saw more coyotes, meadowlarks, white-tail deer, and turtles than ever before in my life. It wasn't always easy to find any animals, and I don't blame them for hiding from the elements. Temperatures ranged from 115°F during summer to frigid winter 5°F with a 25-mile/hr wind that felt like it could blow me right off the planet.

Never in my wildest dreams did I think that the prairie was that diverse, colorful, harsh, and beautiful; and the man that I have to thank for bringing me here is Dr. Jim Shaw. He cheerfully answered a vague letter inquiring about graduate opportunities and has managed to remain cheerful throughout the following 3 years. I appreciate his guidance throughout my studies. My committee member, Dr. David (Chip) Leslie, Jr., was extremely helpful and advised me on a variety of issues related not only to my studies, but my professional development as well. Dr. David Engle provided essential financial assistance, and without him, I would not have been able to complete this study.

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WHERE THE BUFFALO ROAM: IMPLICATIONS FOR THE KEYSTONE SPECIES QUESTION

Abstract.- The concept of keystone species recently has been revised (Power et al. 1996), and bison (*Bos bison*) have been designated a keystone species in tallgrass prairie (Knapp et al. 1999). The problem with this new keystone species definition (i.e., an animal that has a disproportionately large impact relative to its abundance) is that abundance is typically a single measurement (Kotliar 2000). My objective was to examine a seasonally variable bison distribution on a patch-burned tallgrass prairie based on 1) group size and type and 2) burn age and timing of burn. Bison formed substantially larger, mixed groups during summer, and smaller, sexually segregated groups throughout the rest of the year. Bison selected patches burned during the dormant season that were in their 1st post-fire growing season. These areas were selected most often during spring and summer. The combination of large bison herds selectively choosing recently burned areas resulted in a seasonally-variable, concentrated grazing pressure that may substantially alter vegetation. Therefore, an assumption of uniform distribution is not valid in a patch-burned landscape, and abundance should be

measured at multiple scales to determine if bison are truly a keystone species in the tallgrass prairie ecosystem.

Introduction

Bison have been proposed as a keystone species in tallgrass prairie (Knapp et al. 1999). This designation came after Power et al. (1996) revised criteria for defining a keystone species. A keystone species is classified as "one whose effects on community structure or ecosystem processes should be large, and these effects should be large relative to abundance" (Power et al. 1996:609). Keystone species are quantified by a community importance index (CI), which is a proportional change in some designated community or ecosystem trait with respect to abundance of a particular species (Power et al. 1996). This *quantitative measurement* was suggested over more esoteric qualities, such as maintenance of diversity of their particular ecological communities and exceptional importance relative to other species in the community (Mills et al. 1993, Paine 1966). For herbivores, Khanina (1998:1) suggested keystone species should only be those who either "support or essentially alter the main vegetation pattern of the ecosystem." By using a measurement of abundance, keystone species are differentiated from dominant species by having a disproportionately large impact (Power et al. 1996). However, a major drawback with CI is that it typically is measured at a single abundance level for a given habitat. Kotliar (2000) noted that small changes in abundance are capable of substantially changing the CI. Similarly, spatial distributions of species and even

the sampling scale can influence CI values (Kotliar 2000). Consequently, I chose to examine spatial distribution of bison on a landscape-level scale to determine if a single abundance measurement was a prudent method for measuring CI.

Given the current knowledge of bison ecology from northern populations, it is unlikely that bison in southern tallgrass prairie distribute themselves uniformly over the landscape throughout the year because spatial changes in vegetation can affect distribution patterns. Relatively little is known about bison ecology in southern tallgrass prairie because bison have been reintroduced only in the last 1-2 decades after more than a century-long absence (Shaw 1995). Bison and fire are 2 of the primary forces that shape the tallgrass-prairie landscape (Axelrod 1985), and both have been used for restoration of remaining tallgrass prairie (Hamilton 1996). Conway (1989) proposed in cases of restoration, keystone species are essential in reestablishing and maintaining structure and function of the ecosystem. Fire is a vital force in tallgrass prairie for maintaining dominant vegetation and suppressing encroachment by woody vegetation (Fuhlendorf and Engle 2001, Hartnett et al. 1996), but large numbers of bison were not reported in tallgrass prairie in the early 19th century (Botkin 1995, Shaw 1995, Shaw and Lee 1997). Therefore, only present day bison herds are capable of determining bison's keystone species status in this ecosystem.

As bison populations increase in public and private sectors, it is important to decipher mechanisms responsible for differences in distribution (Augustine and McNaughton 1998). Several studies of bison herds have documented seasonal shifts in habitats (Meagher 1973, Melton et al. 1989, Shaw and Carter

1990). Selective feeding behavior in herbivores can be attributed to multiple factors (Plumb and Dodd 1993), including forage availability (Hobbs and Swift 1988), population density (McNaughton 1984), and social organization (Coppedge et al. 1998b). Due to the relatively recent reintroduction of bison to southern tallgrass prairies, investigations of bison in a heterogeneous burned landscape have not been numerous (Coppedge 1996). Potential factors that could impact bison distribution and subsequent abundance include group size, group type, burn history, patch utilization, and plant community (Senft et al. 1987, Steuter et al. 1995, Wallace et al. 1995). All of these factors are interrelated and can vary seasonally.

Seasonal changes in group size are common in ungulates (Bender and Haufler 1999, Marchal et al. 1998), including bison (Meagher 1973, Van Vuren 1983). Group size is often associated with habitat characteristics, such as openness and forage availability (Galland 1989, Morton 1993, Shackleton 1968). A species can vary in group size and composition over a geographic range (Eisenberg 1981). Wood bison (*B. bison athabascae*) and European bison (*B. bonasus*) typically have smaller group sizes and are associated with forested areas (Gębczyńska and Krasińska 1972, Komers and Messier 1993, Krasińska et al. 1987, Melton et al. 1989). Plains bison (*B. bison bison*) typically form large groups during the summer breeding season, with smaller groups occurring throughout the rest of the year (Meagher 1973). Changes in bison group size and type are associated with sexual segregation, with exception of rut when sexes intermingle (Main et al. 1996, Shult 1972). Group types commonly found

include mature males only, females with calves and juveniles, and mixed groups of both sexes (Coppedge 1996, McHugh 1972, Shackleton 1968). These group types are similar to those observed in northern bison herds; however, given the openness of the habitat, it is likely larger groups will form in the tallgrass prairie (Melton et al. 1989, Morton 1993, Soper 1941). Estimates of historic herd sizes, grouping behavior, and general ecology in the southern tallgrass prairie are limited due to the near extinction of bison during the late 19th century (Shaw 1995, Shaw and Lee 1997).

Lack of historic knowledge of bison in this environment is contrasted sharply with the fire history. Fire is thought to be a primary force in shaping tallgrass prairie, along with ungulate grazers (Collins and Wallace 1990, Vinton et al. 1993). Fires were numerous and occurred throughout the year, producing a burn-patch mosaic (Axelrod 1985, Bragg 1982, Collins and Wallace 1990). Time of burning can have pronounced effect on vegetation, with spring burns favoring warm-season perennial grasses, summer burns favoring cool-season perennial grasses and forbs, and autumn burns promoting perennial forbs and sedges (Engle et al. 1998, Towne and Owensby 1984). Despite vegetational differences, Coppedge and Shaw (1998) found limited bison selection for burns of any particular season. Numerous studies have documented bison preference for areas in the 1st growing season after burning (Coppedge and Shaw 1998, Coppock and Detling 1986, Shaw and Carter 1990, Vinton et al. 1993). However, many of these studies did not examine bison use of burns by individual seasons in a complex burn landscape. Temporal and spatial heterogeneity in

resource abundance are likely to influence foraging strategies temporally and spatially (Bergman et al 2001).

Seasonal impacts of bison are not only important for determining effects on plant communities but also for management decisions. Cattle management commonly uses rotational systems to prevent overgrazing of any particular areas and prescribed burns in spring only, which reduces structural and compositional heterogeneity of vegetation (Fuhlendorf and Engle 2001, Towne and Owensby 1984). Cattle and bison differ in foraging selectivity, behavior, and management (Hartnett et al. 1996, Reynolds et al. 1982). Common bison behaviors (grazing, trampling, rubbing, and wallowing) are capable of substantially altering an ecosystem (Edwards 1976, Hartnett et al. 1996, Knapp et al. 1999). A complete understanding of interactions of bison with the fire regime on a year-round basis is necessary when a rotational system is not used. A clear picture of spatial and temporal patterns of habitat use by native herbivores on a landscape level is essential for ecosystem management and restoration (Bailey et al. 1996, Hartnett et al. 1996, Senft et al. 1987).

Investigations of landscape-level effects are often difficult to achieve due to small study areas or human habitat alteration (Larson and Murdock 1989). My study was conducted on 1 of the few remaining unplowed tracts of tallgrass prairie (Hamilton 1996). A spatially random, temporally variable burning regime was used to mimic a natural burn mosaic. The bison herd under investigation had a skewed sex and age ratio, similar to that of commercial bison operations; therefore, this study is applicable to managed bison herds. To assess spatial

and temporal distribution of bison on tallgrass prairie related to the keystone species issue, I had 2 objectives. First, I compared seasonal differences in group sizes and types, and second, I evaluated bison use of burn patches by season, patch age, and season of patch burn. These factors are crucial to the keystone species issue because seasonal distributions can impact bison abundance, which must be taken into account in assessment of ecosystem impact particularly in a complex patch-burned landscape.

Study Area and Methods

Study area

I conducted my research at The Nature Conservancy's 15,342-ha Tallgrass Prairie Preserve (TGPP: 36°50'N, 96°25'W) located 25 km NW of Pawhuska, Oklahoma. Primary vegetation consisted of big bluestem (*Andropogon geradii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*). The Nature Conservancy conducted controlled burns on a random, 3-year return interval during 3 seasons. One-third of the preserve was burned annually, 40% in dormant spring, 20% in summer growing season, and 40% in dormant autumn-winter (Hamilton 1996). Those seasonal burns were broken into smaller patches (1 isolated burn area) using natural and human-made firebreaks. Patches varied in size from 30 to 600 ha and were mapped since their inception in 1993 (Fig. 1). Rainfall during the study period was 10.6% less than average (National Oceanic and Atmospheric Administration 2001, www.noaa.gov). Water was available

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year-round from seasonal creeks and human-made ponds dispersed relatively uniformly throughout the fenced 4,197-ha bison unit. There was no supplemental feeding. Free-choice mineral licks were distributed about 1 per 450 ha throughout the bison unit.

At the beginning of my study in May 2000, there were 869 adult bison with 330 calves, and by the completion of data collection in August 2001, the population numbered 1,197 adults with about 369 calves. The bison herd has a skewed sex and age ratio of 1:5 males to females; one-half of the yearling males were removed annually. Bulls >6.5-years-old and cows >13.5-years-old were culled. This population was controlled by an annual autumn round-up of >95% of the herd.

Data collection

I observed bison on foot or car using 9 x 25 binoculars, starting from a randomly selected point along a 55-km driving route covering the bison unit (Fig. 1). The route was completed every sampling day and was driven at about 10 km/hr. After a bison group was located, I recorded group type, size, composition (sex and age), location on a 1:24,000 United States Geological Survey topographic quadrangle, and burn history of that area (season of burn and burn age). I categorized group types as mixed, bull, or cow-calf groups. Mixed groups consisted of cows, their offspring, and mature and immature bulls (Fuller 1960, Meagher 1973). Bull groups primarily were composed of males >2 years old. Cow-calf groups were made up of cows, young-of-the-year, yearlings,

immature bulls (<2 years old), and ≤2 males >2 years old. I defined groups as cohesive units of ≥2 animals, readily distinguishable as separate entities ≥100 m apart. Mature males often occurred alone and were included in my observations. Sampling for group composition consisted of *ad libitum* census scan samples ≥20 min (Altmann 1974). Larger groups were observed for up to 3 h. Other variables, such at temperature, season, and time of day, were recorded at the beginning of a sampling period. Observational periods were evenly stratified throughout daylight hours. Total number of observations varied seasonally due to differences in the number of groups, although there was relatively equivalent field time. No observations were made in October due to the annual bison round-up.

Data analyses

I defined a sampling unit as 1 bison group. Total number of observations was 1,500, and total observation time was about 885 h. For groups observed twice in 1 day, I did not include the 2nd sample due to a lack of independence. Only adult bison (>1 year old) were included in analyses. Seasons were divided into the following categories: summer (June - September 2000), autumn (November - December 2000), winter (January - February 2001), spring (March - May 2001), and summer 2001 (June - August 2001). An α-value of 0.05 was used for all statistical testing. To examine group size differences by season, I ranked group size as <20, 20–49, 50–99, 100–299, and ≥300 adult animals and analyzed rank by each season in a 5 by 5 contingency table (PROC FREQ, SAS

Institute Inc. 1990). To analyze differences in group sizes in summer 2000 and summer 2001, I used a paired *t*-test (Steel et al. 1997). Similarly, I analyzed counts of group type by season in a 3 by 5 contingency table.

For testing differences in seasonal use of burn patches by patch age and burn season, I calculated a selectivity index value for each burn type by age (Vinton et al. 1993). The selectivity index was the percentage of the total population using a particular patch divided by the proportion of the total area that patch area covers. A total count of all individuals on a patch was chosen for use over a group count due to major group size differences and similar results from group counts (Coppedge 1996). A selectivity index value of 1.0 indicated nonselective use of an area; values >1.0 or <1.0 indicated preference or avoidance of a particular patch type, respectively.

Patch age was determined by the number of growing seasons that an area had experienced, for example, autumn and spring burns were not considered to be in the 1st growing season until 1 March. Summer 2000 burns were included in analyses beginning 1 August 2000. Summer burns were conducted later in 2001 (August – September) so they were not included in analyses for spring and summer 2001. Burned areas that had not yet experienced a growing season were excluded from analyses. Burned areas averaged >450 ha and presumably did not hinder use of an area by another group's presence. If a group covered >1 patch, group size was divided by the number of patches used. Patch ages were calculated for areas 1-, 2-, 3-, and ≥4-years-old by growing season. I analyzed selectivity indices using repeated

measures of season and patch age with a factor analytic covariance structure model, which was chosen because it provided the lowest AIC_c (Akaike's Information Criteria; PROC MIXED, SAS Institute Inc. 1990; Anderson et al. 2000). Burn seasons were analyzed with season and patch age as covariables using an unstructured covariance model in the same manner. Least squares means were calculated for each category of patch and tested for significance using 95% *CI* (Cherry 1996).

Results

Bison group sizes varied by season (X^2 = 403.5, *d.f.* = 16, $P < 0.001$) with groups averaging 205.6 $\pm$ 35.7 *SE* and 195.89 $\pm$ 27.5 for summers 2000 (n = 233) and 2001 (n = 150), respectively. Groups were considerably smaller throughout the rest of the year (autumn: 23.3 $\pm$ 4.5, n = 336; winter: 26.5 $\pm$ 1.7, n = 344; spring: 54.2 $\pm$ 8.8, n = 482). There was no difference between summer 2000 and 2001 group sizes. Group type varied by season with mixed groups most common in summer (81.6% of all groups for summer 2000, 60.3% for summer 2001) and cow-calf (47.4–72.3%) and bull (10.8–19.5%) groups throughout the rest of the year (X^2 = 402.0, *d.f.* = 8, $P < 0.0001$). An average of 75% of the population was located per sampling day, but number of groups observed varied seasonally from an average of 6 groups/day in summer 2001 up to 29 groups/day in winter 2000-2001.

Selectivity indices (AIC_c = 755.8) differed by season across patch ages in spring (F = 9.77; *d.f.* = 3, 102; $P < 0.0001$), summer 2000 (F = 22.01; *d.f.* = 3,

102; $P < 0.0001$), and summer 2001 ($F = 28.09$; *d.f.* = 3, 102; $P < 0.0001$). Across all seasons, only patches in their 1st growing season after burning had differences in usage (1st growing season: $F = 6.00$; *d.f.* = 4, 104; $P < 0.0001$). When "effect slices" (SAS Institute Inc. 1990) are examined together, patches in their 1st growing seasons were used more during spring and summer (Fig. 2A). Autumn was the only season in which patches in their 2nd growing season were used most often, but there were no differences across patch age for autumn ($F = 1.42$; *d.f.* = 3, 102; $P = 0.2386$) and winter ($F = 0.89$; *d.f.* = 3, 102; $P = 0.4505$; Fig. 2B).

Due to significant interactions ($F = 7.89$; *d.f.* = 12, 698; $P < 0.0001$), analysis of burn seasons was separated by patch age and season ($AIC_c = 904.5$). For patches in their 1st growing season (Fig. 3), spring burns were used disproportionately more in the 2 summers ($P < 0.05$) but in proportion throughout the rest of the year. Summer burns were used less than expected for all available seasons ($P < 0.05$). Autumn burns were never used more than expected, but the most use occurred during spring and summers. Patches in their 2nd growing season were used less than expected, regardless of burn season or season ($P < 0.05$). For patches in their 3rd growing season, all burns were used less than expected ($P < 0.05$). Summer burns in their 2nd and 3rd growing seasons were used slightly more during autumn, winter, and spring. Finally, for patches in their 4th growing season or older, all available burns were underused in all seasons ($P < 0.05$). Unburned areas (patches not burned in since 1993) never received substantial use during any season ($P < 0.05$).

DISCUSSION

A difficulty in quantifying bison distribution lies in the interactions of seasonal grouping behaviors because average bison group sizes and group types differ seasonally. Bison groups at the TGPP were largest during summer and smaller in autumn and winter. These groups were the largest bison groups on record (McHugh 1972, Meagher 1973, Shackleton 1968, Shult 1972, Van Vuren 1983), which is likely related to abundant available and patchily distributed forage (Fryxell 1991, Morton 1993). Mixed groups are the largest group type and are found most often in spring and summer, coinciding with the primary growing season of the vegetation. Despite increased population size, which resulted in a higher density, the difference in group sizes between summer 2000 and 2001 was negligible. I observed that large groups, composed of several hundred animals, were transitory, often lasting less than a day and would splinter into smaller sub-units that varied in size from 10 to >100 animals (McHugh 1972). Most studies of bison behavior find that the largest groups occur during rut (Meagher 1973, Shackleton 1968, Shult 1972), but in tallgrass prairie, bison formed herds >300 individuals (25–35% of the total population) 2–3 months prior to the onset of rut. After rutting behavior subsides in September, bison once again broke into smaller (1/16th to 1/4th the size of mixed herds), sexually segregated groups. While bison are gregarious and influenced by group membership, extended herd cohesion is not common (Van Vuren 1983). Thus,

group membership is not necessarily a factor in selection of foraging sites (Wallace et al. 1995).

Group size has a substantial impact on the ecological impacts of bison (Shaw and Lee 1997), and concentration of groups on particular patches can intensify these effects. Initial examination of seasonal use of burned areas in my study indicated a strong preference for recently burned areas during spring and summer, as has been found frequently in similar studies (Coppedge and Shaw 1998, Nellis and Briggs 1997). However, patch use was more variable by time since burn during autumn and winter. At Konza Prairie in autumn and winter, 20-year-old burns were used more than during the growing season, but the entire area was grazed more evenly (Vinton et al. 1993) than at TGPP. That pattern was probably related to the burn return interval at Konza with only a few areas burned on an annual or biannual basis (Knapp et al. 1999). At the TGPP, bison distribution is highly variable by season. Mixed groups of >300 bison occur almost exclusively on burned areas during the growing season. Nellis and Briggs (1997), using a coefficient of localization, also found increased relative concentration of bison from April to August on Konza Prairie. Throughout the rest of the year, smaller groups are more widely dispersed over more patches of varying age (Fryxell 1991, Vinton et al. 1993), which results in disproportionate grazing pressure on recently burned areas (Fuhlendorf and Engle 2001). A temporally variable and concentrated density of bison during the growing season does not result in a uniform grazing pressure and potentially poses substantial ecological changes in tallgrass prairie.

Because bison showed distinct seasonal preferences for patches of different age and time of burn, a temporal scale must be taken into account in not only grouping activities but also grazing. In spring and summer, areas in their 1st growing season were used most often, comparable to other studies on burned tallgrass prairie (Coppedge 1996, Larson and Murdock 1989, Nellis and Briggs 1997). Burned watersheds at Konza Prairie were used up to 3 times more often than unburned patches, particularly in spring (Vinton et al. 1993). Comparing burns by season, there was a similar pattern of burn selection between the 2 summers, but burns in summer 2001 had a much higher selectivity for 1st-year growing season than in summer 2000 (Fig. 2A). This was likely due to higher herd densities as the population increased in relation to less total burned area. For seasonal burns, new spring burns were selected most often in summer and were used proportionately throughout the rest of the year. However, summer burns were never used as often as expected, regardless of burn age or season. Autumn burns were used in proportion to availability during spring and both summers but not during autumn and winter. That pattern presumably demonstrated the gramnivorous habits of bison (Plumb and Dodd 1993), illustrated in their burn season selection. In contrast to Coppedge (1996), bison selected spring burns most often, followed by autumn burns and summer burns, during their 1st growing season, in accordance with the decreasing trend in mean graminoid:forb biomass ratio.

All patches >1-year-old were used less in proportion to availability. While areas in their 1st growing season were used most often throughout the entire

year, there were some seasonal changes in selection trends of patches. Autumn was the only season in which areas in their 2nd growing season were used most often. Because 1st-year burns are used so heavily during summer, bison may regraze to the previous year's burns during autumn. Use of summer burns increased slightly during winter of the 2nd and 3rd growing season and spring of the 3rd growing season, which may have been related to growth of cool-season vegetation. Spring and autumn burns showed variable use with increasing age, which is probably related to burn age preference by bison. Unburned areas always were used less than expected as shown in previous research (Coppedge 1996). Therefore, seasonal burning influenced bison distribution, particularly with respect to burn age.

Undisputedly, bison interact with fire (Fuhlendorf and Engle 2001), but mechanisms behind burn selection by bison are not well understood. Knapp et al. (1999) suggested more research was necessary for identification of factors influencing grazing patch selection. Generally, large ungulates feed randomly within a patch but select areas for grazing based on forage abundance at landscape scales (Wallace et al. 1995). Incorporating fire into tallgrass prairie alters the plant community, particularly by the season of burning. Therefore, individual patches have differences in forage characteristics based on when they were burned. Specifically, spring burns and unburned areas have the highest relative composition of tallgrasses while summer burns have the highest levels of annual grasses, forbs, and legumes (Coppedge 1996, Engle et al. 1998). Burning in spring increases production of dominant grasses and decreases

detritus, which both influence bison grazing (Coppock et al. 1983). Presumably, these factors resulted in heavy selection by bison during summer. However, unburned areas were not selected, despite having the greatest proportion of dominant tallgrasses. Vinton et al. (1993) found infrequently burned tallgrass prairie (20-year interval) had the highest level of C_3 grasses. It is likely forb abundance and accumulation of detritus deters bison grazing in those areas (Pfeiffer and Hartnett 1995).

In contrast to early dormant-season fires, fires during the growing season reduce the competitive ability of warm season species and favor cool season plants (Howe 1994). Summer burns were not used as heavily as other burns, which may be due to a greater percentage of forb cover (Engle et al. 1998, Plumb and Dodd 1993, Vinton et al. 1993) removal of dominant bunchgrasses (Engle et al. 2000), or low vegetation growth rates from less than average rainfall. Autumn burns are similar to spring burns because they are both conducted during the dormant season, which promotes dominant C_4 grasses. Autumn burns promote growth of sedges (Coppedge and Shaw 1998), which are cool season graminoids. Sedges typically grow during cool-season and moist periods of the year (Howe 1994) and are a common component of bison diets on tallgrass prairie but vary by season (Coppedge 1996).

Seasonal analyses of bison diets indicated that bison alter forage choices depending on latitude (Popp 1981). Bison in northern Canada foraged in wet meadows, consuming grasses and sedges in proportion to their abundance (Larter and Gates 1987, Reynolds et al. 1978); bison in Yellowstone National

Park also chose grasses and sedges throughout the year (Meagher 1973). At Wind Cave National Park, Popp (1981) found that bison selected cool-season graminoids much of the year, with increased warm-season grasses during summer. Bison in the tallgrass prairie show a strong selectivity for grasses during the majority of the year and sedges in winter and spring (Coppedge et al. 1998b). Sedges were chosen more in winter and spring (20-39% of the diet) than summer and autumn (11-15%), which corresponded to seasonal availability of sedges (Coppedge 1996). Digestibility of sedges tends to decrease as the growing season advances (Bergman et al. 2001). Consequently, bison appear to eat more sedges during winter and spring when they are more easily digested but only show substantial use of autumn burns that promote cool-season graminoids during spring. Consequently, forage maturation appears to influence bison selectivity and subsequent distribution (Fryxell 1991).

Habitat selection has been the focus of numerous wildlife studies, but in this case, selection is occurring at finer, patch-level scale in continuous grassland. Nutrition found in native tallgrasses is variable by season (Waller et al. 1972), regardless of burning, and season appears to influence patch selection. Plant growth generally begins in early spring (2nd to 3rd week in March), with the majority of growth occurring between April and August (Dwyer 1961). The most vigorous growth is during late spring and early summer, if ample rainfall occurs (Coppedge et al. 1998a, Waller et al. 1972). Plants with a C_4 photosynthetic pathway (typically warm season plants) tend to have lower nutrient yield, and instead of avoidance, bison favored C_4 plants as the growing

season advanced (Steuter et al. 1995). This was illustrated in the equal use of spring and autumn burns in spring, with a shift toward increased use of spring burns later in summer. Late spring burns (typically burned in May) tend to increase standing crop of big bluestem later in the growing season (Mitchell et al. 1996). Bison appear to take advantage of vigorous growth in summer by selecting new burns that are producing the highest biomass (Coppedge et al. 1998a, Fulendorf and Engle 2001), thereby avoiding detritus and maintaining grazing lawns (McNaughton 1984).

In mid-July to early August, tallgrasses mature and produce seeds, and by early autumn, plants are dormant and lignified (Waller et al. 1972). After plants mature in August, selection for newly burned areas decreases but is still greater than older burns. Autumn and winter had the least selectivity. In winter, random feeding patterns decrease movement and conserve energy, particularly when forage quality is low (Wallace et al. 1995). With limited high-quality forage available in autumn and winter, large herbivores feed in areas where they can increase intake (Bailey et al. 1996, Demment and Van Soest 1985). Larson and Murdock (1989) found bison used high biomass areas, which were unburned and unmowed, most often from October through February. Given availability of new burns for bison at TGPP, bison probably do not have to resort to low-quality, high-quantity unburned areas.

In complex burned habitat, such as the TGPP, bison selectivity was expected to vary with respect to burn season, associated vegetational characteristics, and season, but there may have been other factors that were not

examined. The most prominent trend was bison preference for burns in their 1st growing season that were conducted during the dormant season. Despite analyses that account for patch size, bison tend to use larger patches for a greater period of time (Coppedge 1996). A larger number of patches were burned at TGPP during the dormant season, and many of those were larger in area than available growing season burns. Therefore, patch size may have been a confounding variable. Coppedge et al. (1998a) found that areas used by bison showed a negative relationship between phytomass and grazing intensity, which was unexpected due to the high productivity of this ecosystem. Bison use recent burns even after they are virtually devoid of vegetation (K. L. Schuler, pers. obs.), but whether they continue to use that area because it has the highest forage quality or if it provides easier access to forage is unknown. Likewise on Konza Prairie, bison regraze patches throughout the year rather than developing new grazed areas (Vinton and Harnett 1992). It is apparent that bison have a substantial impact on newly burned areas, most prominently during summer, and these impacts are localized to particular areas. Bison managers planning to implement a seasonally variable, patch-burn system should take into account bison preferences and grouping behavior in determining when and where to conduct burns because bison grazing intensity and seasonal burn type are capable of substantially influencing ensuing vegetation (Coppedge et al. 1998a). Maximization of diversity can be accomplished through conscientious use of bison and fire (Fuhlendorf and Engle 2001), but to what extent this interaction affects bison keystone species standing still remains to be known.

Relating this to the keystone species issue (Knapp et al. 1999), there is a distinct difference in abundance by season and patch type. This creates a problem in declaring bison a keystone species because their impact may not be disproportionately large relative to their increased abundance on particular areas (Kotliar 2000). Depending on the scale used to measure changes in vegetation, recently burned versus unburned or season of burn, there could be considerable effects due to disproportionately heavy use by bison in particular burned patches compared with more uniform distribution in unburned areas. Ungrazed patches in tallgrass prairie usually are more homogeneous than moderately grazed areas because dominant plants, such as big bluestem, create dense stands of biomass that reduce structural diversity (Fuhlendorf and Engle 2001). In heavily used areas, bison are capable of modifying long-term plant growth through repeated defoliation (Augustine and McNaughton 1998, Vinton and Hartnett 1992). Spatial distribution of ungulates can influence ecological processes at several levels besides grazing patch selection; these can include juxtaposition of patches, nutrient turnover, forage consumption, soil disturbance, and vegetational trampling (Damhoureyeh and Hartnett 1997, Huntly 1991, Wallace et al. 1995).

Perhaps the greatest challenge lies in assessing the time scale required to accurately measure the impact of changes by species' abundance (Power et al. 1996). If bison no longer use an area, how long do their impacts last? Knapp et al. (1999) cited historic bison wallows as evidence of long-term changes, but there is debate over whether historic bison wallows are really historic (England and DeVos 1969) or if they are merely soil-specific depressions (Coppedge et al.

1999). Unfortunately, historic evidence of bison in tallgrass prairie is incapable of providing a base level of bison abundance to apply to the keystone species issue (Botkin 1995, England and De Vos 1969, Shaw 1995, Shaw and Lee 1997).

For present day herds, a bison-use history for a specific area should be established before applying uniform abundance rates to randomly chosen comparisons of vegetation. In burned tallgrass prairie, bison have a spatially and temporally nonrandom distribution that localizes their impacts (Steuter et al. 1995), and it must be accounted for in determination of bison as a keystone species. Similar to Kotliar (2000), I suggest a multiscale approach to determining keystone species, rather than a single measurement of abundance and inclusion of an additional standard: keystone species provide unique functions or roles not carried out by any other organism or mechanism. To this end, comprehensive investigation of changes produced from vegetational communities in wallows, horning of woody vegetation, and nutrient cycling through carcasses, dung, and urine could provide further evidence of the bison's keystone role. If historically estimated low numbers of bison are more indicative of true populations in southern tallgrass prairie (Botkin 1995, Shaw and Lee 1997) than the widely held belief of bison numbering in the millions (McHugh 1972), efforts at restoration of bison may actually be altering the biome, producing an ecosystem that does not actually represent the original tallgrass prairie.

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Fig. 1 - Burn mosaic by year and season of burn and driving route at Tallgrass Prairie Preserve. Newer burns are darker; unburned areas are shown in white.

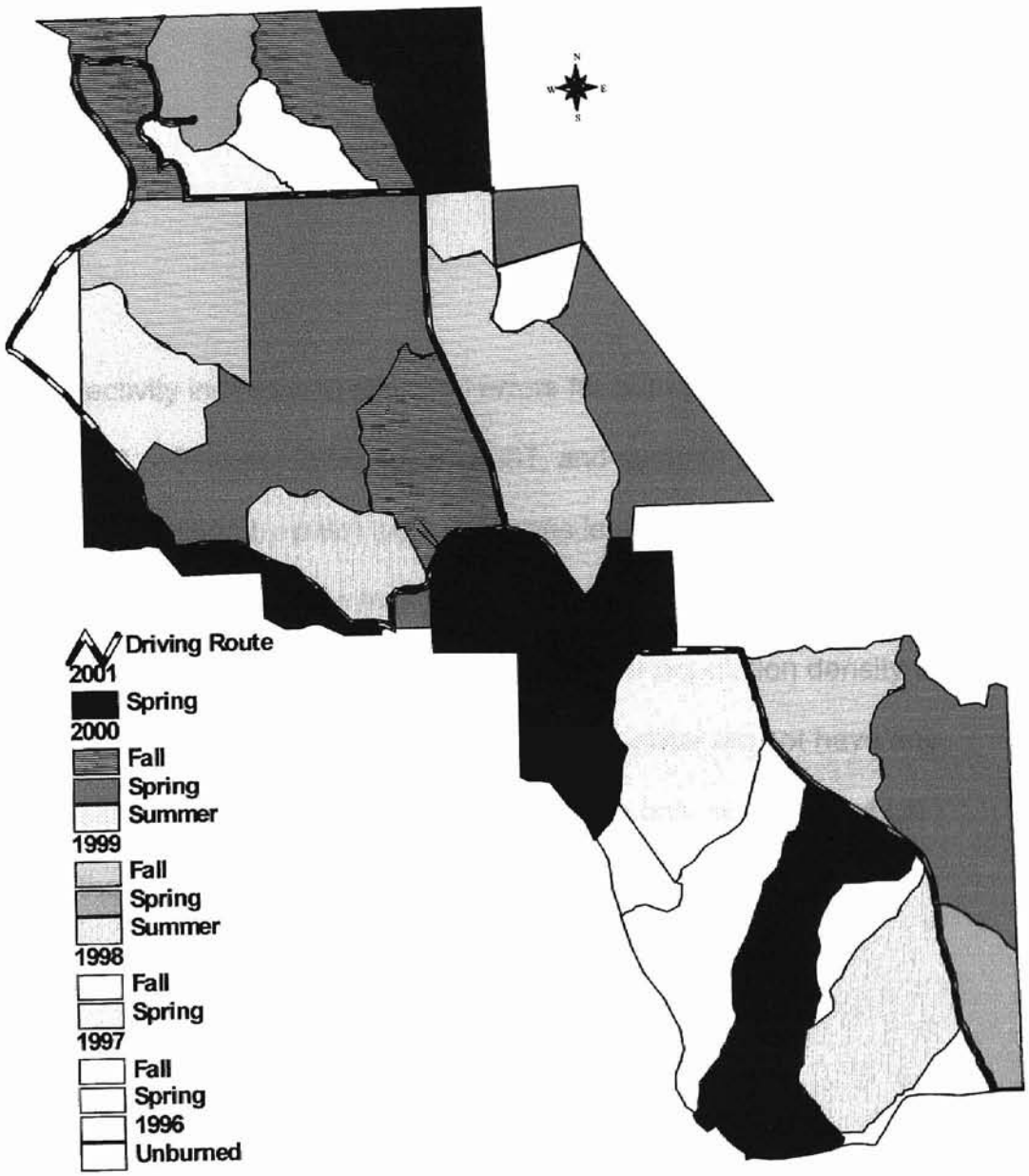

Driving Route
2001
Spring
2000
Fall
Spring
Summer
1999
Fall
Spring
Summer
1998
Fall
Spring
1997
Fall
Spring
1996
Unburned

Fig. 2. - Selectivity indices and standard errors for burn patches by patch age and season. A. - Summer 2000, spring 2001, and summer 2001 showed differences in selection by patch age with areas in their 1st post-fire growing season used significantly more than expected based on availability. Differences between the 2 summers were attributable to a higher population density and a lower proportion of burned areas. B.- Autumn and winter did not have any differential selection by patch age. Autumn was the only season in which patches in their 2nd growing season were used most often.

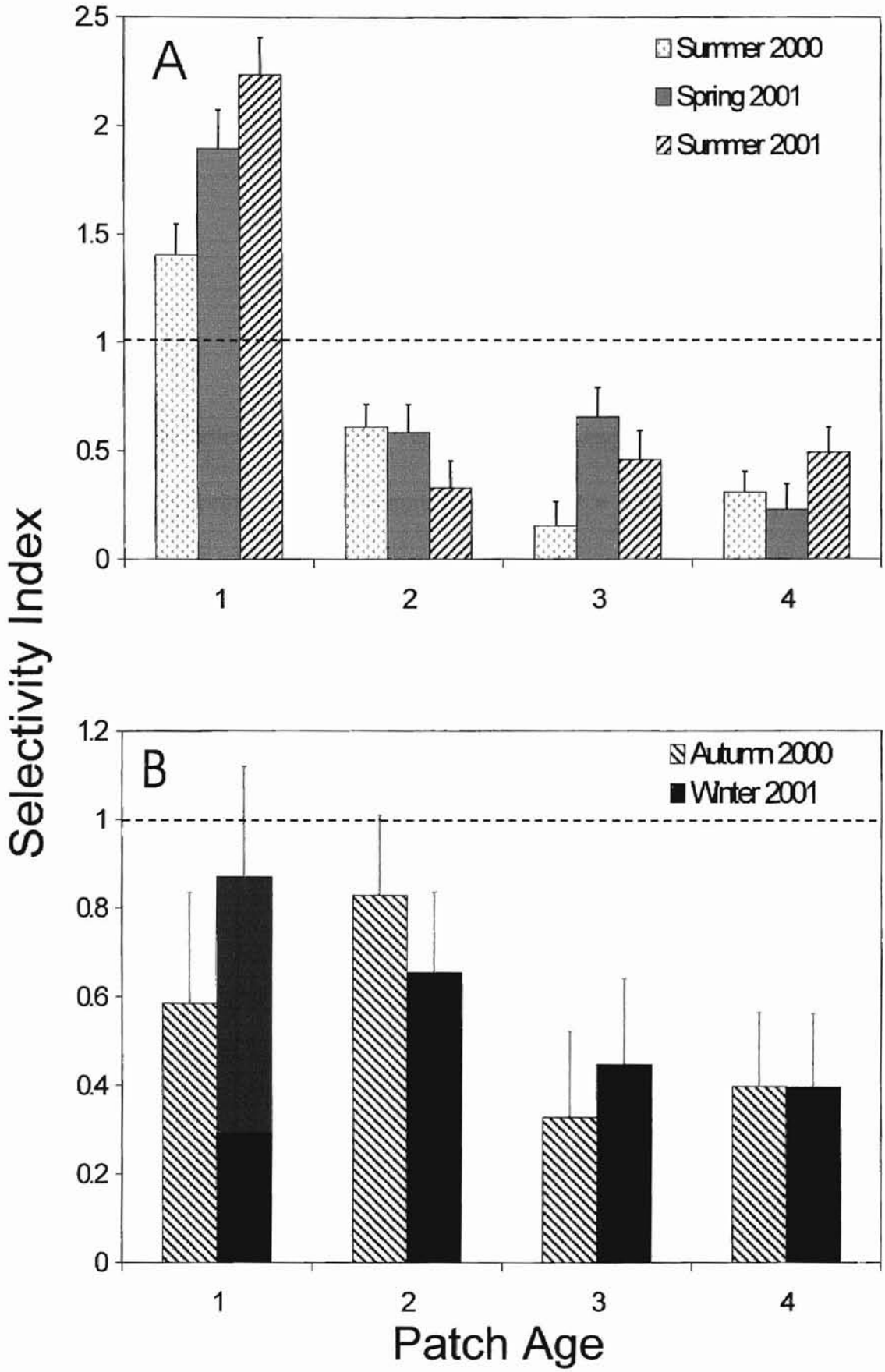
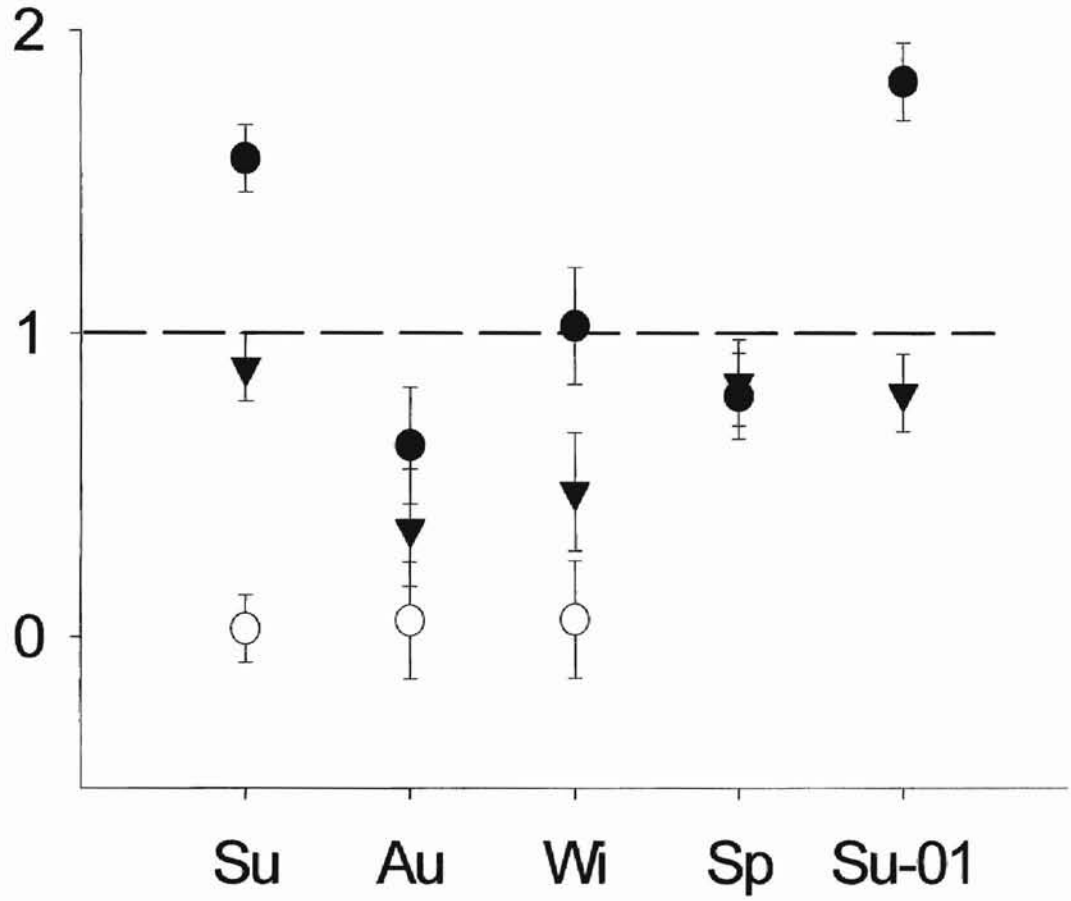

A
Summer 2000
Spring 2001
Summer 2001
2.5
2
1.5
1
0.5
0
1
2
3
4
B
Autumn 2000
Winter 2001
1.2
1
0.8
0.6
0.4
0.2
0
1
2
3
4
Selectivity Index
Patch Age

Fig. 3 - Selectivity indices and *SE* for 1st post-fire growing season burns by timing of burn [● = spring burns, ○ = summer burns, ▼ = autumn burns]. Spring burns were preferred more often in both summers and selected proportionally with availability throughout the rest of the year. Summer burns (Su and Su-01) were avoided when available. Autumn (Au) burns were selected proportionally in spring (Sp) and both summers, but not autumn and winter (Wi).


2
1
0
Su
Au
Wi
Sp
Su-01

CHAPTER II

AN ORDINATION ANALYSIS OF BISON GROUP BEHAVIOR ON OKLAHOMA TALLGRASS PRAIRIE

Abstract. - Sexual segregation commonly occurs in ungulates with males and females living separately outside rut. Bison (*Bos bison*) divide into bull and cow-calf groups throughout most of the year, and mixed groups are found primarily during late spring and summer. My objective was to investigate differences in bison group behavior in relation to several variables: group type, group size, season, time of day, temperature, and burn characteristics (season of burn, burn size, and burn age). I tested behavioral variability among grazing, moving, standing, lying, wallowing, and rubbing using partial redundancy analysis (pRDA) with Monte Carlo permutation tests. Two results lend support to the sexual dimorphism–body size hypothesis of sexual segregation: cow-calf groups were correlated positively with grazing while bull groups were related more closely to ruminating activities. For all groups, posture while ruminating differed by season; standing occurred more often in summer presumably permitting heat dissipation, and lying down in winter for heat conservation. Most movement occurred during summer by cow-calf groups crossing areas not recently burned. Bison sought newly burned patches to graze and foraged more in larger burn areas.

Ordination techniques explained variation in several behaviors related to ecology of bison in tallgrass prairie.

Introduction

Bison groups are dynamic and generally are not well understood (Van Vuren 1983). Bison have a strong drive to aggregate and are herd animals, with exception of a few solitary bulls (McHugh 1972, Shaw and Meagher 1999, Van Vuren 1983). Group associations are variable by sex, but bison typically are gregarious. Sexual segregation is commonly found in wild, north-temperate ruminants (Ruckstahl 1998) and is subject to social, spatial, and temporal influences (Main et al. 1996). Bison are sexually segregated, with the exception of rut when smaller units come together to form large, mixed groups (Reynolds et al. 1982, Shaw and Meagher 1999). Throughout the year, group size tends to vary for unknown reasons (McHugh 1972, Van Vuren 1983). Number, composition, and stability of groups also are quite variable (Reynolds et al. 1982, Van Vuren 1983, Lott and Minta 1983). Individual behavioral variations may be responsible for differences observed in various group types.

Bison group types typically are associated with particular seasons, and behavioral changes correlated with season. Seasonal cycles in energy metabolism are common in temperate and arctic wild ruminants and likely exist in bison (Christopherson and Hudson 1978). Bison reduce metabolic rates and overall activity at extremely cold temperatures (-30°C — Christopherson et al. 1978), and northern bison herds limit movements in winter (Meagher 1973). In

general, bison are noted for mobility but are not considered migratory (McHugh 1972, Roe 1970, Shaw and Meagher 1999). A unique bison behavior is creation of wallows, which increases in frequency in summer on tallgrass prairie (Coppedge 1996). Wallows are formed by trampling and dust-bathing (Polley and Wallace 1986), possibly as an aggressive gesture, an escape from biting flies, a tick-defense strategy, or shedding process to remove winter pelage (McHugh 1972, Reynolds et al. 1982, Mooring and Samuel 1998, McMillan et al. 2000). Seasonal rubbing may be related to shedding and insect harassment that frequently occurs in summer (Coppedge and Shaw 1997, Reynolds et al. 1982).

While season may alter bison behavior, a landscape-level burn mosaic also may influence bison activities. Foraging is primarily a diurnal activity (McHugh 1972), and fire regime, plant structure, and group composition can dictate grazing locations (Vinton et al. 1993). Burn areas tend to have more rapid initial growth (Coppock and Detling 1986, Nellis and Briggs 1997) and higher forage quality (Coppock et al. 1983) and quantity (Wallace et al. 1995) than unburned areas. Previous studies in tallgrass prairie found that bison selectively use newly burned areas during the 1st post-fire growing season and then avoid those areas and concentrate on newer burns (Catchpole 1996, Coppedge and Shaw 1998a, Hartnett et al. 1996, Nellis and Briggs 1997). However, those studies were conducted at finer scales and lack the complex burn distributional pattern of this study area.

Interactions of bison and fire in tallgrass prairie have been the focus of many studies in the past decade since bison reintroduction, but bison behavior in

this area has received little attention (Meagher 1978, Reynolds et al. 1982, Knapp et al. 1999). My objective was to investigate differences in bison group behavior as related to several explanatory variables. I tested the following hypotheses: 1) different types of bison groups vary their activities due to the sex and age of individuals in that group; 2) bison vary behavior by season in response to temperature; 3) bison favor new burns over older burns; 4) bison prefer larger burn areas; and 5) bison selectivity for burn patches differ with season of burn.

Study Area and Methods

Study area

I conducted this research at The Nature Conservancy's 15,342-ha Tallgrass Prairie Preserve (36°50'N, 96°25'W) located 25-km NW of Pawhuska, Oklahoma. Primary vegetation consisted of big bluestem (*Andropogon geradii*), little bluestem (*Schizachyrium scoparium*), switchgrass (*Panicum virgatum*), and indiangrass (*Sorghastrum nutans*). The Nature Conservancy performed controlled burns on a random, 3-year return interval during 3 seasons. One-third of the preserve was burned annually: 40% in dormant spring, 20% in summer growing season, and 40% in dormant autumn/winter (Hamilton 1996). Water was available year-round from seasonal creeks and man-made ponds dispersed relatively uniformly throughout the fenced 4,197-ha bison unit. At the beginning of my study in May 2000, there were 869 adult bison with 330 calves, and by the

completion of data collection in August 2001, the population numbered 1,123 adults with 369 calves. The bison herd had a skewed sex and age ratio of 1:5 males to females; one-half of the yearling males were removed annually. Bulls >6.5-years-old and cows >13.5-years-old were culled. This population was controlled by an annual autumn round-up of >95% of the herd.

Data collection

I observed bison by foot or car using 9 x 25 binoculars, starting from a randomly selected point along a 55-km driving route covering the bison unit. This route was completed every sampling day and was driven at about 10 km/h. After a bison group was located, I recorded group type, size, composition (sex and age), behavior, location on a 1:24,000 United States Geological Survey topographic quadrangle, and burn history of that area (season of burn and burn age). I categorized group types as mixed, bull, or cow-calf groups. Mixed groups consisted of cows, their offspring, and mature and immature bulls. Bull groups were composed primarily of males >2 years old. Cow-calf groups were made up of cows, young-of-the-year, yearlings, immature bulls (<2 years old), and ≤2 males >2 years old. I defined groups as cohesive units of ≥2 animals, readily distinguishable as disparate entities separated by an ocular estimate ≥100 m. Mature males often occurred alone and were included in my observations. Sampling for group composition and behavior consisted of *ad libitum* census scan samples ≥20 min (Altmann 1974). Larger groups were observed for longer time periods (≤3 h). Behavioral observations and

explanatory variables, such as temperature, season, and time of day, were recorded at the beginning of a sampling period. Observational periods were evenly stratified throughout daylight hours. Total number of observations varied seasonally, despite relatively equivalent field time, due to differences in group size. No observations were made in October due to the annual bison round-up.

I evaluated bison behavior by estimating the percentage of the group engaged in a particular activity. Those activities were grazing, moving, lying, standing, wallowing, and rubbing. I classified grazing and moving as active behaviors, and lying and standing were inactive, presumably ruminating or resting, behaviors (Dwyer 1961). Wallowing and rubbing were considered rare, special behaviors performed by individual animals, not the group as a whole. Grazing was recorded if an animal was foraging or moving with their head close to ground level. Moving was noted if an animal was traveling with their head up. I recorded lying if the ventral side was in contact with the ground. Wallowing was defined as an animal dropping to the ground and rolling on its back with its legs in the air ≥2 successive times. Wallowing was distinctively different than lying. Rubbing also was a unique behavior in which a bison would rub their head, horns, neck, or body on any vertical or horizontal structure.

Data analyses

I defined a sampling unit as an observation of a bison group. Total observation time was about 885 h resulting in 1,500 group observations. For groups observed twice in 1 day, I did not include 2nd samples due to possible

lack of independence. To examine group size differences by season, I ranked group size as <20, 20–49, 50–99, 100–299, and ≥300 adult animals and analyzed rank by season in a 5 by 5 contingency table (PROC FREQ; SAS Institute Inc. 1990). Summer 2000 and summer 2001 were kept separate due to differences in population density and were compared with a paired *t*-test, regardless of group type (Steel et al. 1997). Similarly, group type was analyzed by season in a 3 by 5 contingency table (PROC FREQ; SAS Institute Inc. 1990).

Testing these hypotheses with a large number of variables traditionally requires numerous traditional statistical tests, but from such analyses, a complete picture of bison behavior would be difficult to achieve (De Miguel et al. 1997). Therefore, I used multivariate ordination techniques to reduce the number of multiple comparisons that would otherwise be necessary in individual analyses (Sokal and Rohlf 1969, Zar 1974, Zolman 1993). Specifically, I chose partial redundancy analysis (pRDA), which is an extension of multiple regression, to model multivariate responses (ter Braak 1986, Legendre and Legendre 1998). Compared with other multivariate tests, pRDA uses a constrained, linear statistical model to position behavioral responses with respect to test variables (Lepš and Šmilauer 2000). The pRDA permits estimation of variation in behaviors attributable solely to 1 variable, by factoring out variation due to covariables. Because pRDA was a direct gradient analysis, I tested influences of explanatory variables on behavior patterns. The variables included: group type (mixed, bull, cow-calf), group size, season (summer, autumn, winter, spring), time of day, temperature, and burn characteristics (season of burn, burn age, and

burn size). Multivariate analyses are commonly used in community ecology to detect and explain environmental gradients (Palmer 1993, ter Braak and Prentice 1988) and have been successfully but infrequently used to identify patterns in behavioral data (De Miguel et al. 1997, Kazmaier et al. 2001).

All behavioral data received a square-root transformation but were not downweighted by rare behaviors (ter Braak 1987). Data were centered but not standardized. I used CANOCO version 3.12 (ter Braak 1987) for analyses. All axes in pRDA were tested using Monte Carlo analysis with 999 permutations at $\alpha = 0.05$ and corrected using the Bonferroni method. Ordination diagrams were created using CANODRAW 5.0 (Šmilaur 2001). Ordination biplots were displayed with behaviors shown by arrows in the direction that behavior increases. Quantitative explanatory variables also were shown as arrows directed toward increasing values, while qualitative explanatory variables were represented as centroids (Lepš and Šmilauer 2000). Behavioral arrows directed toward centroids or in a similar direction as explanatory arrows were correlated positively; conversely, those directed away were correlated negatively (Lepš and Šmilauer 2000). Arrows or centroids closer to the origin of the coordinate system corresponded to an average value of the explanatory variable being tested (Lepš and Šmilauer 2000).

Results

All bison groups, regardless of group type, were larger in summer (Table 1) than in all other seasons ($\chi^2 = 403.5$, *d.f.* = 16, $P < 0.0001$). There was no difference between group sizes in summers 2000 and 2001. Group types (Table

1) differed by season ($\chi^2 = 402.0$, *d.f.* = 8, $P < 0.0001$). Mixed groups were most common in summer and sometimes included all individuals accounted for that day. Cow-calf and bull groups were found most frequently in autumn, winter, and spring.

For ordination analysis, I tested the null hypothesis that bison group types had similar behaviors. To control for effects of other variables, I included variables not directly tested in the analysis as covariables. All axes were significant ($P = 0.002$), indicating patterns differed from random. The pRDA axis 1 most likely represented a gradient in sex as cow-calf and bull groups represented 2 extremes and mixed groups were intermediate (Fig. 1-A). While this type of analysis does not provide individual *P*-values, interpretation of these significant axes is relevant. The ordination diagram of group type and behavior indicated mixed groups were related positively to all behaviors except for movement ($n = 291$). Grazing ($n = 1,218$) was associated positively with cow-calf groups and negatively with bull groups. Conversely, bull groups were related positively to lying ($n = 602$), whereas cow-calf groups had a negative relationship. Mixed groups corresponded positively to standing ($n = 336$), rubbing ($n = 203$), and wallowing ($n = 187$).

To further control for seasonal influences associated with group type, I repeated each analysis for individual seasons using burn characteristics as covariables. Of all seasons, spring provided the only significant axes ($P = 0.018$). Similar to analysis for all seasons, mixed groups were associated positively with wallowing, rubbing, and lying down in spring (Fig. 1-B). Mixed

groups were uncorrelated with grazing and standing, and grazing and movement were positively related to cow-calf groups. Bull groups were uncorrelated with movement and negatively correlated with grazing. In contrast to the ordination of all seasons combined, bull groups were associated positively with standing rather than lying.

Because mixed groups tended to be larger than bull or cow-calf groups, I investigated influence of group size individually with a null hypothesis that behavior would not differ between dissimilar size groups. Group type, season, and burn characteristics were used as covariables; group type, season, and season of burn also were blocking variables. Wallowing and rubbing were associated positively with increasing group size, standing was related positively, and most other behaviors were not correlated (Table 2).

To test the null hypothesis that bison behaviors did not vary among seasons, group types and burn characteristics were used as covariables and blocks for analysis of seasonal effects on behavior. Interpretation of the ordination diagram (Fig. 2) indicated summer was associated positively with movement, wallowing, standing, and less so with rubbing. Spring was associated positively with grazing and negatively with standing. Standing was related more closely to autumn and lying in winter. Autumn and winter were correlated negatively with grazing.

To investigate effects of time of day and temperature, I conducted a pRDA for each using season, burn characteristics, and group type as covariables and blocks. My null hypotheses were that neither time of day nor temperature

influenced bison behavior. Movement was associated positively with increasing time of day, grazing was related positively, and all other behaviors were not correlated (Table 2). In contrast, standing, lying, wallowing, and rubbing exhibited positive associations with increasing temperature, while movement and grazing were related negatively (Table 2).

Finally, I tested if burned patch properties (season, size, age) resulted in behavioral variations. Monte Carlo analysis of a pRDA for burn characteristic indicated that the pattern differed from random ($P = 0.002$). Most notably, movement was associated positively with increasing burn age (Fig. 3). Those areas also were correlated negatively with wallowing, rubbing, and grazing. Grazing was associated positively with increasing size of burned areas; standing and lying down were related negatively to burn size and coupled positively with spring burns. Spring burns also showed increased wallowing activity, which was not associated to summer burns and correlated negatively to autumn burns.

Discussion

Bison behaviors were simultaneously influenced by several variables. Grazing was most often observed and was most commonly associated with cow-calf groups and less with bull groups. Cow-calf groups are nutritionally stressed by pregnancy, lactation demands, and forage requirements for young animals (Shaw and Carter 1989). Bull groups consisted of mature males that did not spend as much time grazing as cow-calf groups. In analysis by season, grazing was correlated most strongly with spring. This is the time of maximum

productivity in the southern tallgrass prairie (Adams and Wallace 1985, Waller et al. 1972) and is a critical time for animals to restore energy reserves depleted during winter. Sexual segregation theory suggests segregation should peak when habitat choice most significantly impacts physical condition, and there is a large range of requirements for reproductive success (Main et al. 1996). For most ungulates, the critical period is spring-summer (Main et al. 1996) when males are preparing for rut (Mautz 1978), and females are giving birth, lactating, and nursing young (Shaw and Carter 1989). In support of this finding, my analysis yielded only 1 season, spring, in which group-type behavior differed significantly from random. In spring, cow-calf groups were related positively to grazing and movement. It is possible that this movement reflected females seeking new sources of quality forage.

Conversely, bull groups were likely to ruminate more often in spring. This finding could support the sexual dimorphism–body size hypothesis, where females are more likely to forage on low-fiber, high-quality grasses, while males prefer abundant, low-quality forage (Post et al. 2001). In tallgrass prairie, preference of females is for newly burned areas while males use patches that have not recently burned and have a higher biomass (Coppedge and Shaw 1998b). Typically, forage quality decreases with increased plant maturity and biomass (Van Soest 1982), and the sexual dimorphism–body size hypothesis represents a trade-off between forage quality and quantity (Hobbs and Swift 1988). Male ungulates are capable of more efficiently converting high-fiber, low-quality forage into energy due to their larger ruminoreticular volume (Demment

1982, Gordon and Illius 1994). Less digestible forages remain in the rumen longer than those that are easily digested (Robbins 1993). This pattern may explain tendencies of bull groups to engage in ruminating activities more often than grazing. If activity budgets of animals differ, it is unlikely those animals will remain together in a group (Galland 1989, Komers et al. 1993).

Most bison in a group performed active behaviors at the same time, but I usually found ruminating behaviors (standing or lying down) together in a group. Standing was highly variable and mostly likely represented an intermediate activity between grazing and lying for rumination or rest. Compared with grazing, energetic costs of rumination are small, with standing slightly more energetically costly than lying (Osuji 1974, Rutley and Hudson 2000). Mixed groups throughout the year and bull groups during spring were associated strongly and positively with standing. Males in bull and mixed groups may prefer to stand in spring to better detect potential mates or rivals. Summer, increased temperature, and group size were all correlated positively with standing. Bison produce more heat from rumination in spring than in autumn (Galbraith et al. 1998), which may induce stress in the animals when combined with high temperatures.

Different postures for rumination may be a behavioral means of thermoregulation. Standing permits bison to dissipate more heat from their ventral side than when they lie down to ruminate (Dwyer 1961, Melton et al. 1989, Moen 1968). Moose (*Alces alces*) had higher heat production while lying in summer than winter (Regelin et al. 1985). Heat loss is dictated by surface area, which is determined by body posture (Robbins 1993). Greater exposure of

surface area while standing reduces thermal insulation of the animal's body (Gates and Hudson 1979). Bison were often found in large groups standing and laying around and in ponds during high temperatures (Dwyer 1961). Lying was associated strongly with autumn and winter, when conservation of heat can be important. In elk (*Cervus elphus*), lying animals had 2-3 times greater thermal insulation than standing and active animals (Gates and Hudson 1979). Autumn and winter were associated negatively with grazing and moving, but snow cover probably did not impede foraging or movement. It is doubtful bison in southern tallgrass prairie are extremely cold-stressed because the lowest temperature recorded in the field was -15°C. However, bison appear to be thermally stressed by high temperature because they resort to panting for heat dissipation and reduced activity, when summer air temperatures reached 42°C. Similarly, elk and mule deer (*Odocoileus hemionus*) increase respiratory rates as a function of ambient temperature with open-mouth panting occurring at upper critical thermal temperatures of 26–35°C in summer (Parker and Robbins 1984).

Despite apparent thermal stress, movement occurred most often during summer. Cow-calf groups moved the most of all groups in spring. Plausible explanations include searching for quality forage, traversing from 1 burn location to another (Coppedge 1996), or locating suitable calving sites, although bison are less secretive than elk in their choice of calving locations (Bian and West 1997, Vore and Schmidt 2001). Movement also was correlated with temperature and time of day. Bison often moved to a new patch in late afternoon. The most significant movement took place on unburned areas and patches of increasing

time since last burn. Those were lower quality forage areas and were by-passed for fresh burn patches that provided higher quality forage. Coppedge's (1996) study in the tallgrass prairie indicated that bison grazing also was related negatively with burn age.

Unburned areas also appear to be avoided for wallowing and rubbing because they were used less often for grazing. Wallowing and rubbing showed distinct trends, but specific causes for these behaviors could not be determined. These behaviors occurred primarily in large mixed groups during summer. Unfortunately, the most influential of these 3 factors (mixed groups, summer, and large group sizes) could not be separated. Similarly, it was not possible to distinguish between stimuli for wallowing and rubbing. Bison are more likely to suffer from insect harassment in summer, and large groups of bison may attract more insects (McMillan et al. 2000). I did note that calves increased frequency of rubbing when shedding their 1st hair coat; they typically did not wallow or suffer as much harassment from flies as adults did in summer (McMillan et al. 2000).

Wallowing and rubbing behaviors are known to alter ecosystems (Collins and Uno 1983, Coppedge and Shaw 1997, Gibson 1986, Polley and Collins 1984, Polley and Wallace 1986). Additionally, grazing plays a major role in determining composition of vegetation (Knapp et al. 1999). Foraging theory predicts that large burned patches should have longer residence time by grazers (Stephen and Krebs 1993). While my study did not incorporate time spent in each patch, positive association of grazing with increasing burn size indicated more grazing occurred in larger areas (Fig. 3). Previous studies in tallgrass

prairie found positive relationships between burn size and grazing patterns (Coppedge 1996). There was no discernable variation in burn season, despite differences in characteristics of vegetation (Coppedge and Shaw 1998a). In this situation, univariate techniques may be more adept at clarifying behavioral differences on seasonal burns than multivariate techniques.

Ordination assessed independent effects of several highly correlated variables, and incorporated more rare behaviors (e.g., wallowing, rubbing) with substantially fewer tests than the numerous multiple comparisons that would have been required in univariate analyses. Ordination techniques were conducive to analysis of complex behavioral relationships (Kazmaier et al. 2001), and extensive data sets with copious variables can be easily deciphered for hypothesis generation or statistical testing (Lepš and Šmilauer 2000). While traditional multivariate techniques are not new to behavioral studies (Duvall et al. 1985, Call et al. 1999, Beeching 1997, Wiltenmuth and Nishikawa 1998), no other studies of behavior have used pRDA to decipher roles of variables in explaining variations in behavior (De Miguel et al. 1997, Kazmaier et al. 2001). In this case, ordination biplots demonstrated that group type, season, temperature, and burn characteristics all are capable of influencing behavior. Social, temporal, and spatial ecology must be considered for meaningful interpretation of bison behaviors.

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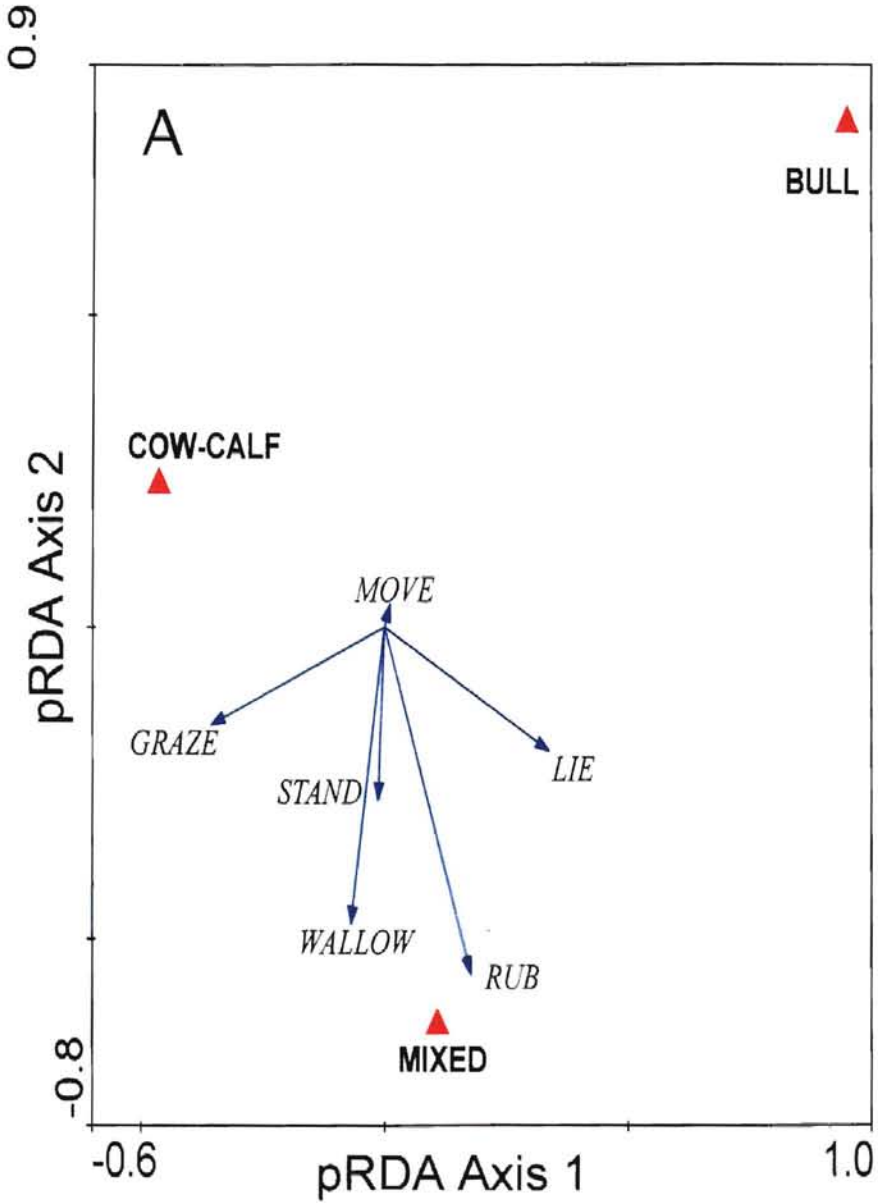
Table 1. – Group size for bison by season and group type at the Tallgrass Prairie Preserve, Oklahoma; only adult animals were included.

			Mixed			Cow-Calf			Bull		
Year	Season	Months	n	Mean	SE	n	Mean	SE	n	Mean	SE
2000	Summer	Jun-Sep	186	136.4	12.0	15	36.7	21.5	15	2.0	0.3
	Autumn	Nov-Dec	45	24.9	3.3	215	28.3	2.2	52	4.2	0.4
2001	Winter	Jan-Feb	51	55.3	8.7	221	27.5	1.5	32	6.7	1.0
	Spring	Mar-May	154	107.1	12.5	230	26.2	1.6	91	5.9	0.5
	Summer	Jun-Aug	91	285.0	32.2	25	18.2	4.5	35	1.3	0.1

Table 2. – Behavioral scores ("species" scores in ter Braak 1986) for group size, time of day, and temperature. Higher scores, relative to scores in that category, indicate stronger positive or negative relationships. Scores closer to zero represent behaviors uncorrelated with particular explanatory variables. Because a pRDA was performed for each individual explanatory variable, the 1st axis explained 100% of variation in the constrained ordination. The 1st axis of group size was significant at $P = 0.002$ ($F = 37.153$). Time of day provided a marginally nonsignificant canonical axis ($F = 2.883$, $P = 0.06$). Temperature had significance at Bonferroni adjusted $P = 0.002$ ($F = 37.153$), the 1st axis had an eigenvalue of 0.023.

Behavior	Group Size	Time of Day	Temperature
Graze	0.0212	-0.0413	-0.1400
Move	0.0205	0.0709	-0.0431
Lay	0.0602	-0.0186	0.2190
Stand	0.1059	-0.0191	0.1199
Wallow	0.3232	-0.0170	0.1082
Rub	0.2429	-0.0129	0.0682

Fig. 1. A. - pRDA of bison behavior by group type with covariables of season and burn types. The first 2 axes accounted for 97.9% of explained variation. Monte Carlo analysis of the 1st canonical axis had an eigenvalue of 0.005 (F = 7.539, P = 0.006), and the sum of all canonical axes (0.007) was significant at P = 0.002 (F = 3.650) indicating behaviors differed from random. B. - The pRDA biplot of spring-only bison behaviors by group type. All axes were significant (1st canonical axis: F = 7.539, P = 0.018; all canonical axes: F = 3.650, P = 0.004). The first 2 axes of the spring-only ordination accounted for 95.7% of the explained variance, with eigenvalues of 0.014 and 0.004, respectively.


A
0.9
-0.8
pRDA Axis 2
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BULL
COW-CALF
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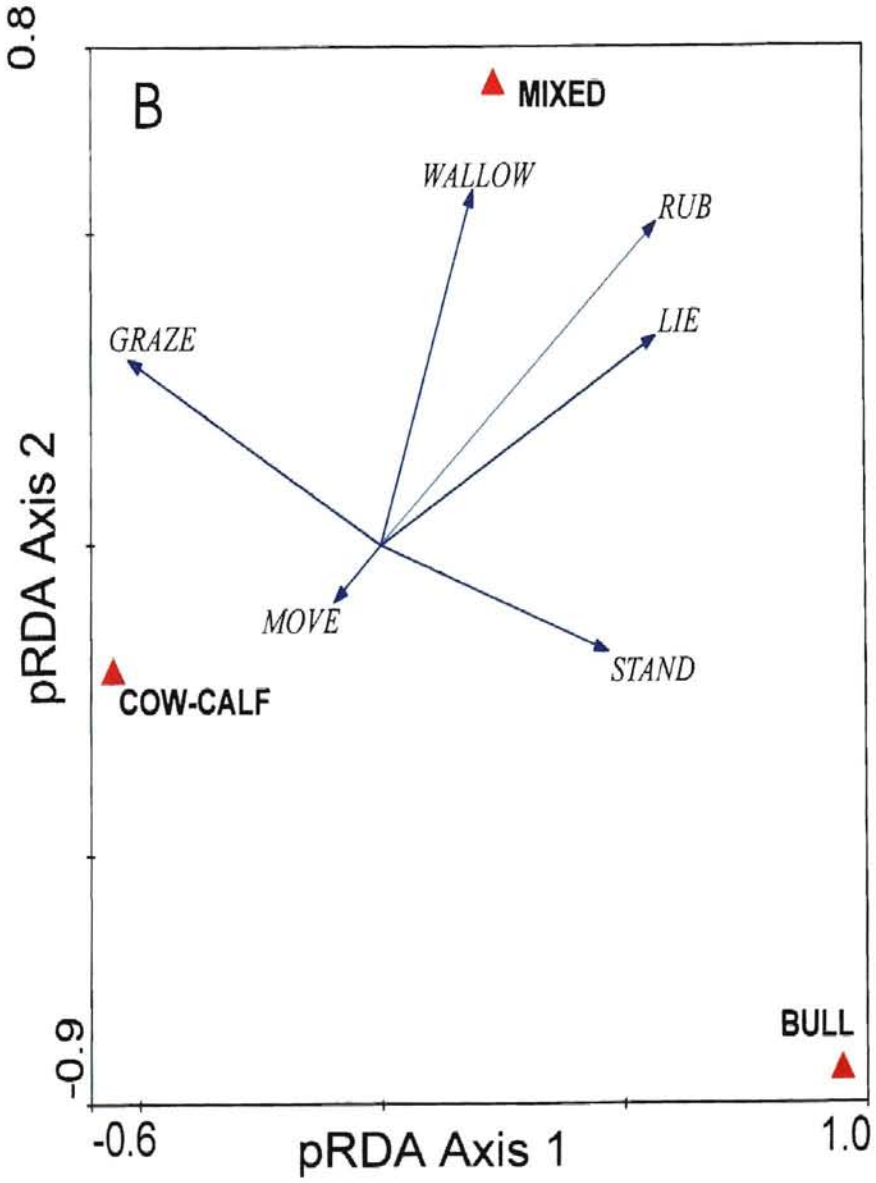

B
0.8
-0.9
pRDA Axis 2
-0.6
pRDA Axis 1
1.0
MIXED
WALLOW
RUB
LIE
GRAZE
MOVE
STAND
COW-CALF
BULL

Fig. 2 - Biplot of pRDA for bison behavior among seasons. Ordination axes 1 (eigenvalue = 0.008, 64.7% of variance) and 2 (eigenvalue = 0.004, 34.5% of variance) explained 99.2% of variation in the data. The 1st (F = 7.539) and all canonical axes (F = 3.650) were significant at P = 0.002.

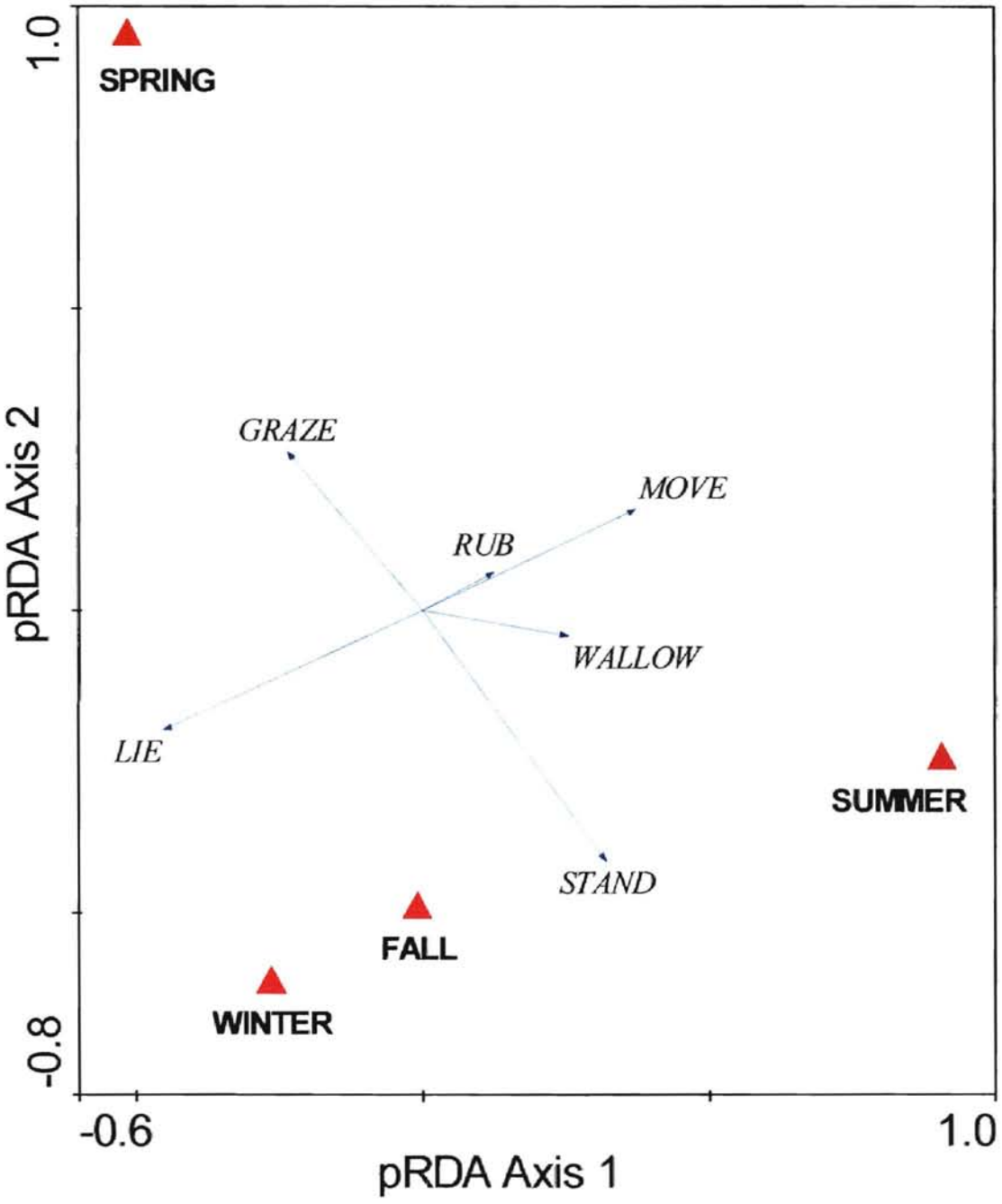
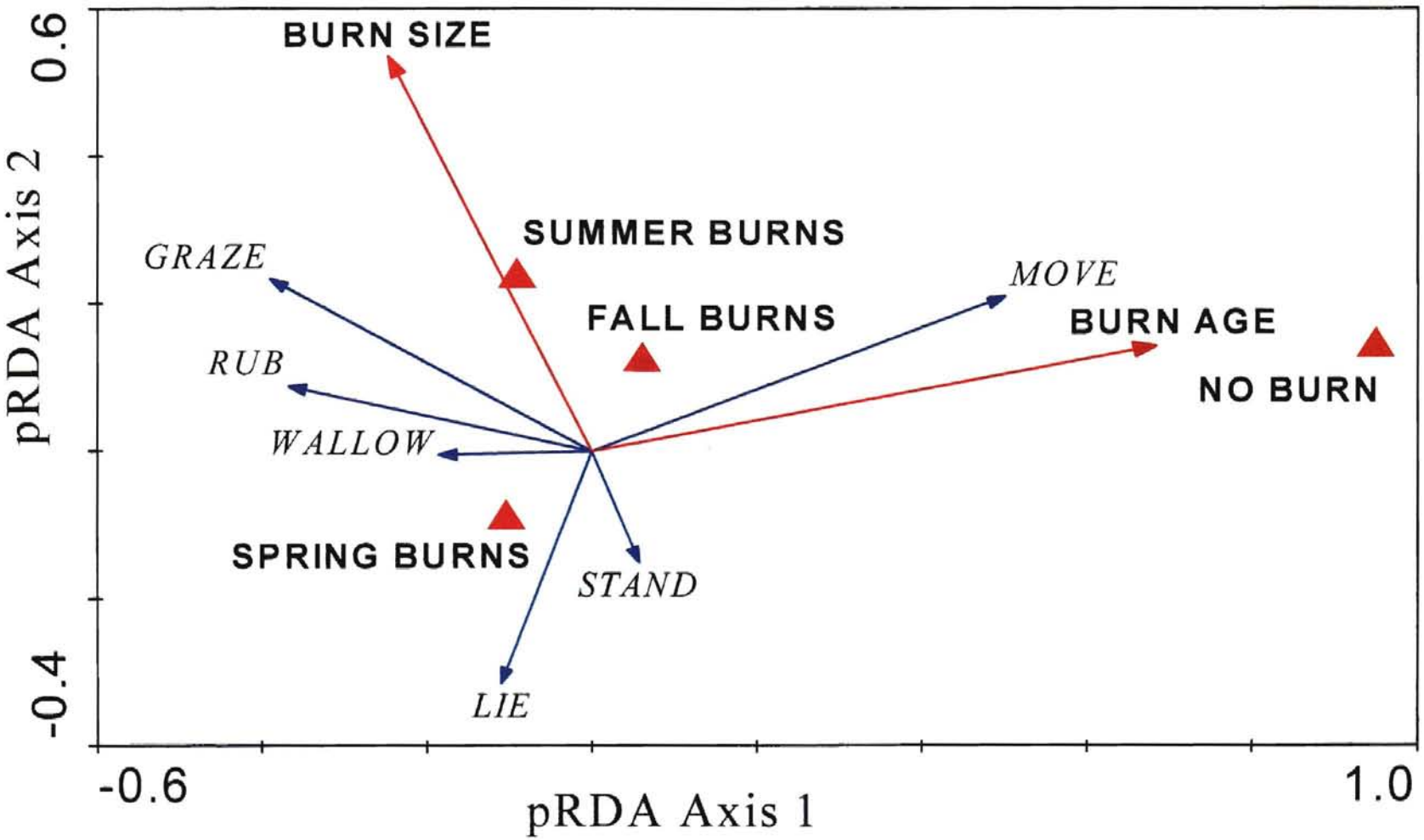

1.0
SPRING
GRAZE
MOVE
RUB
WALLOW
LIE
SUMMER
STAND
FALL
WINTER
-0.8
pRDA Axis 2
-0.6
1.0
pRDA Axis 1

Fig. 3 - The pRDA of burn season, burn size, and burn age as environmental variables. Monte Carlo analysis yielded significant axes (F = 10.886, P = 0.004 for the 1st canonical axis; F = 3.142, P = 0.002 for all canonical axes) when effects of season and group type were controlled. The eigenvalues for the first 4 axes were 0.007, 0.004, 0.001, and 0.000, respectively.


BURN SIZE
SUMMER BURNS
GRAZE
MOVE
FALL BURNS
BURN AGE
RUB
NO BURN
WALLOW
SPRING BURNS
STAND
LIE
0.6
-0.4
pRDA Axis 2
-0.6
1.0
pRDA Axis 1

VITA

Krysten Lynn Schuler 2

Candidate for the Degree of

Master of Science

Thesis: SEASONAL VARIATION IN BISON DISTRIBUTION AND GROUP BEHAVIOR IN OKLAHOMA TALLGRASS PRAIRIE

Major Field: Wildlife & Fisheries Ecology

Biographical:

Personal Data: Born in Pittsburgh, Pennsylvania, on January 29, 1976, the daughter of Michael and Diane Schuler

Education: Graduated from Bradford Area High School, Bradford, Pennsylvania in May 1994; received a Bachelor of Science degree in Biological Sciences from the University of Notre Dame, Notre Dame, Indiana, in May 1998; completed the requirements for the Master of Science degree in Wildlife Ecology from Oklahoma State University, Stillwater, Oklahoma, in May 2002.

Professional Experience: Laboratory Technician, Department of Otolaryngology, University of Pittsburgh, August 1998 to August 1999; Graduate Teaching Assistant, Department of Zoology, Oklahoma State University, August 1999 to May 2002.

Professional Organizations: The Wildlife Society, American Society of Mammalogists, Oklahoma Academy of Sciences.